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A botanical inventory of a submontane tropical rainforest on Negros Island, Philippines

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Abstract. This paper provides a botanical inventory of a forest community in the North Negros Forest Reserve that is disproportionately valuable from a conservation perspective. The forest fragment is one of the last remaining wet tropical rainforest ecosystems in the biogeographic region of the West Visayas and an important refuge for a large number of endemic species. Using standard methods of the Philippine Plant Inventory Project we described the structure and composition of this little known forest type in the transition zone between lowland and lower montane forest. A 1 ha inventory plot 500 × 20 m in size was established and all trees of 10 cm DBH or greater were measured and permanently labeled. Subsequently, fertile specimens were collected over a period of 18 months. We found 645 individuals belonging to 92 species, 54 genera and 39 families with a combined basal area of 58.8 m^2 and an average canopy height of 30 m. This community was not dominated by dipterocarps. Species of Lauraceae, Burseraceae, Sapotaceae and Icainaceae were equally or more important. Diversity measured as Shannon–Wiener index (5.59), equitability index (0.86) and Simpson index (0.032) was high, and no single family or species dominated the plot.

Key words: botanical inventory, conservation, forest trees, Philippines

Introduction

Due to their economic importance, lowland dipterocarp forests in Southeast Asia have been studied quite extensively, and research has been reviewed, for example, by Whitmore (1984), Kartawinata (1989), and Soepadmo (1995). Only a small number of studies, however, have been conducted in the submontane and montane forest regions, and particularly the Philippine mountain ranges have hardly been explored (Ashton 1993). Detailed botanical work in these forest communities is limited to an earlier work by Brown (1919) on Luzon and a recent study on Mindanao (Pipoly and Madulid 1998).

Being the last remaining forest fragments in the Philippines, montane and submontane ecosystems have recently become the focus of attention for conservation efforts (Heaney 1993; Penafiel 1994). Particularly forests fragments of the central Philippine islands, including Panay, Guimaras, Negros, Cebu and Masbate, fall into the IUCN category of the highest conservation priority (Dinerstein et al. 1995), and have also been identified as centers of plant biodiversity (Davis 1995). Cebu, Masbate, and Guimaras have been completely deforested, whereas small forest fragments remain on Panay and Negros. The North Negros Forest Reserve with an original area of 80 500 ha contains today's largest fragment of evergreen rain forest in the central Philippine islands. A recent survey, however, revealed that in the insufficiently protected reserve only 9800 ha of submontane and montane old-growth forest are remaining, while all lowland dipterocarp forest has been illegally cleared (Figure 1). The remaining fragment is an important refuge for a great number of endemic wildlife species, and conservation projects and captive breeding programs have been launched to save at least some of the species from extinction (Heaney 1993; Oliver 1993; Curio et al. 1996).

The aim of the present study is to evaluate the structure and composition of species of this submontane ecosystem. As part of a conservation project in this region the study shall provide a botanical reference for ongoing ecological research and conservation efforts in the North Negros Forest Reserve. Further, we want to extend the botanical knowledge about high elevation forest communities in the Southeast Asian region.

Materials and methods

Study site

The inventory was conducted within a submontane tropical rain forest in the North Negros Forest Reserve on the island of Negros, 10°41′ N, 123°11′ E (Figure 1). The study area lies on the northwest slope of Mt. Mandalagan on volcanic soils at an elevation of 1000 m above sea level. The forest reserve probably does not contain truly undisturbed primary forest, but at the study site cutting of trees was prevented by the steep topography and difficult logistics for logging companies. Weather records from this mountain range are only available for one year with a total rainfall of 4650 mm and an average temperature of 25.4 °C. There was a less rainy period around the month of April. This period, however, is not dry enough to create any deciduousness in the forest.

Mapping and identification

We established a 1 ha inventory plot, 500 × 20 m in size and divided into 20 × 20 m subplots with biodegradable vinyl flagging. Subsequently we measured all trees with 10 cm dbh or more, permanently tagged them with aluminum labels, and collected voucher specimens in triplicate for all fertile individuals and in duplicate for sterile trees. In cases where it was possible to identify a specimen unambiguously as having

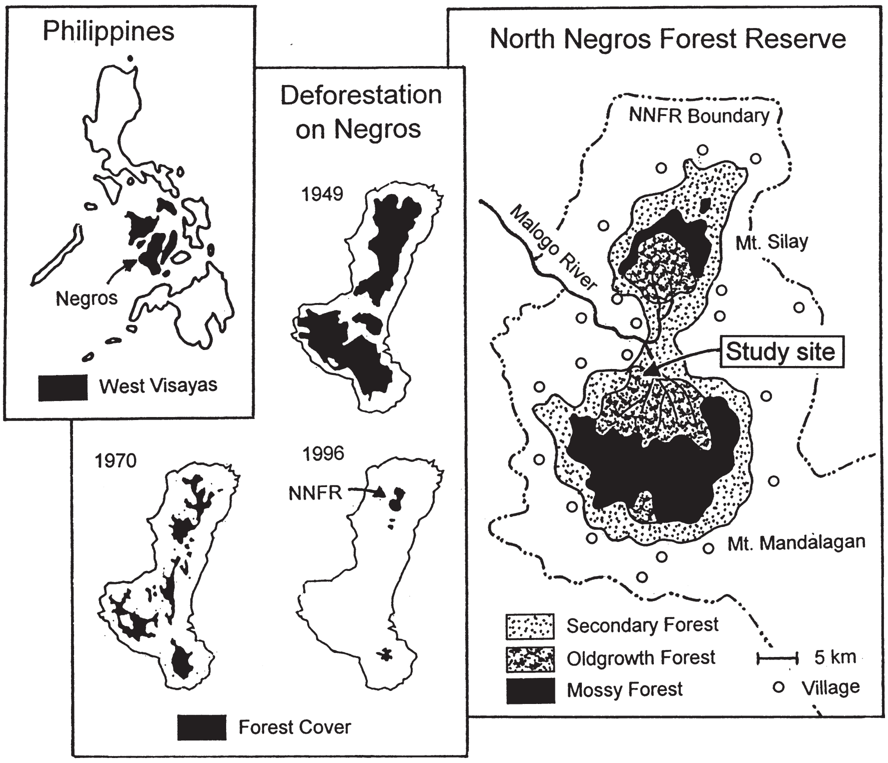

Figure 1. Location of the study site (10°41′ N, 123°11′ E) and deforestation on Negros and in the North Negros Forest Reserve according to government documents and a survey in 1996.

been three times previously collected, the sample was discarded, leaving sets of 220 specimens from this inventory. In order to obtain fertile material from as many individuals as possible we revisited the plot several times from August 1995 to January 1998. In addition to dried specimens, flowers and fruits were also preserved in 70% alcohol. A botanical collection has been deposited at West Visayas State University, Panay and the Philippine National Museum, Manila. A set of selected specimens was transferred to the Rijksherbarium, Leiden, Netherlands for specialist identification.

Forest description

All methods were chosen in accordance with those used in the Philippine Plant Inventory Project (Madulid 1996; Pipoly and Madulid 1998) to provide results comparable with other studies in the region. For every species we calculated the following values: (1) relative frequency, which is the number of subplots in which a species occurs divided by the sum of occurrences of all species in subplots; (2) relative density, which is the number of trees of a species divided by the number of all trees;

(3) relative dominance, which is the basal area of one species divided by the combined plot basal area; (4) an importance value, which was calculated by summation of relative frequency, relative density and relative dominance.

Further, we assigned a dispersal syndrome to each species according to the type of its fruits based on Van der Pijl (1982). A fruit was considered bird dispersed, when indehiscent, red or black in color and of small to medium size, or when dehiscent with arilate seeds. Odorous fruits of dull color, born on large branches or stems and of medium size were considered fruit-bat dispersed. Large juicy fruits with few well protected seeds were classified as fruits dispersed by mammals. Dehiscent, winged fruits were classified as wind dispersed, and all fruits that did not fall into any of these categories were classified as miscellaneous. Further, we rated all species according to their crown position based on Richards (1982). Tree species were divided into species predominantly in the euphotic zone, in which the crowns are more or less fully exposed to sunlight, and those in the shaded oligophotic zone beneath. A species was in the first category, if at least one individual exceeded a height of 25 m and had a dominant or codominant crown position. Otherwise the species was rated as understory tree, unless clearly described as canopy tree in the botanical literature.

Tree species abundance in the forest community was described by means of diversity indices. Three commonly used indices were calculated according to Hill (1973):
(1) the Shannon–Wiener index: $H = -\sum(n_i/N)\log_2(n_i/N)$,
(2) the equitability index: $E = H/\log_2 s$,
(3) the Simpson index: $S = \sum(n_i/N)^2$,
where n_i is the number of individuals of species i, N is the total number of individuals, and s is the total number of species on the plot.

Species abundance was further quantified through a $\log_2$ frequency distribution of the number of species containing 1, 2, 3–4, 5–8... individuals. The portion of species captured by the 1 ha sample was estimated using a species-area relation, based on the number of species found on plots of increasing size. The cumulative number of species was plotted over the combined plot area each time a 20 × 20 m subplot was added. The curve represents means of two counts from both ends of the plot.

Results

General description

We found 645 individuals with a combined basal area of 58.8 m^2 on the inventory plot, belonging to 92 species, 54 genera and 39 families. The average canopy height was 30 m with exceptional trees reaching a height of 40 m. Truly emergent trees were rare. The species area relation (Figure 2) suggests that the sample captured a large portion of the species richness, since the curve fairly levels off at 1 ha. Table 1

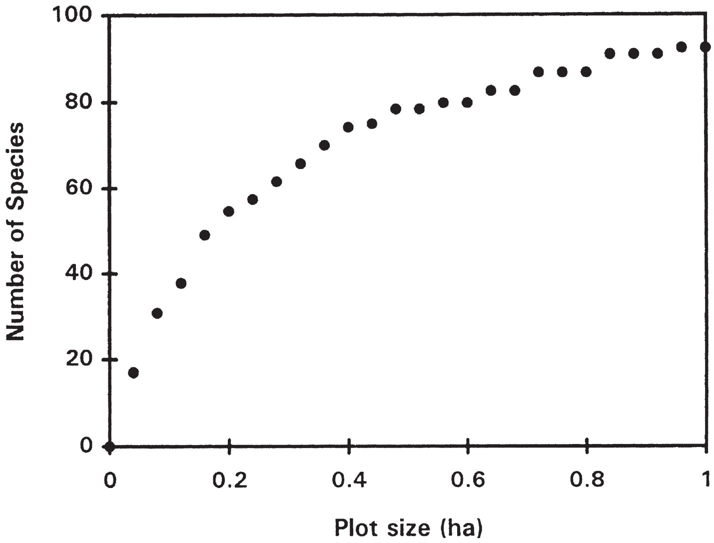

Figure 2. Species–area relation based on a cumulative species count on 20 × 20 m subplots of a 1 ha inventory plot.

lists these species by family and shows frequency, basal area, relative density, relative dominance, importance values for each species as well as family totals. In addition ecological information is given on the dispersal syndrome and the crown position of each tree species. Species diversity indices were 5.59 (Shannon–Wiener) and 0.032 (Simpson). The evenness of species abundance was described by an equitability index of 0.86 and by the frequency distribution shown in Figure 3. Two-thirds of the species were represented by four or fewer individuals on the plot, while only three species fell into the class of 33–64 individuals which accounted for 15% of all trees.

Species composition

The 10 most important species accounted for almost half of the combined importance value (Table 2). Similarly the 10 most important families included species that made up for almost three-quarters of the combined importance values. No single species or family clearly dominated the plot. Dipterocarpaceae, Lauraceae, Sapotaceae, Burseraceae and Melastomaceae as the five most important families accounted each for around 10% of the total importance value, whereas the most important species had relative importance values ranging from 4 to 8%. Although few canopy trees were members of the families Moraceae and Euphorbiaceae, these families had high importance values due to the high frequency of individuals. With 56 individuals *Litsea luzonica* was the most frequent tree, followed by *Canarium asperum, Platea excelsa* and *Palaquium* sp. with 52, 37 and 23 individuals, respectively. With 12% relative dominance *Litsea luzonica* contributed most to the basal area, followed by *Shorea*

Table 1. Number of trees, basal area (sqm), relative frequency, relative density, relative dominance, importance values, dispersal syndrome (w = wind, g = gravity, b = bird, f = fruitbat, m = mammal), and crown position (c = canopy-top, u = understory) for tree species of a 1 ha inventory plot.

Family Species	Collection Number	No. of trees	Basal area	Rel. freq.	Rel. dens.	Rel. dom.	I.V.	Disp. synd.	Crown pos.
Aceraceae									
Acer niveum Bl.	N-437	7	0.349	1.44	1.09	0.59	3.12	w	c
Actinidiaceae									
Saurauia polysperma (Blco.) Merr.	N-105	1	0.009	0.21	0.16	0.02	0.38	?	u
Anacardiaceae									
Semecarpus glauciphyllus Elm.	N-070	3	0.295	0.62	0.47	0.50	1.59	?	c
Araliaceae									
Schefflera octophyllum (Thunb.) Nakai	N-141	1	0.032	0.21	0.16	0.05	0.42	?	u
Araucariaceae									
Agathis philippinensis Warb.	N-534	11	0.752	2.06	1.71	1.28	5.05	g	c
Burseraceae									
Canarium asperum Bth.	N-694	52	5.202	4.95	8.06	8.84	21.85	b	c
Canarium villosum Bth. & Hook	N-477	3	0.124	0.62	0.47	0.21	1.29	b	c
Family total:		55	5.326	5.57	8.53	9.05	23.15		
Celastraceae									
Siphonodon celastrineus Griff.	N-417	8	0.201	1.24	1.24	0.34	2.82	b	u
Compositae									
Vernonia arborea Buch.-Ham.	N-163	1	0.113	0.21	0.16	0.19	0.55	w	c
Cunoniaceae									
Caldcluvia celebica (Bl.) Hoogl.	N-164	2	0.129	0.41	0.31	0.22	0.94	?	c
Weinmania camiguinensis Elm.	N-159	3	0.938	0.62	0.47	1.59	2.68	b	c
Family total:		5	1.067	1.03	0.78	1.81	3.62		
Dilleniaceae									
Dillenia philippinensis Rolfe	N-642	2	0.316	0.41	0.31	0.54	1.26	m	c
Dillenia reifferscheidia Elm.	N-055	3	0.048	0.41	0.47	0.08	0.96	m	c
Family total:		5	0.364	0.82	0.78	0.62	2.22		

Table 1. Continued.

Family Species	Collection Number	No. of trees	Basal area	Rel. freq.	Rel. dens.	Rel. dom.	I.V.	Disp. synd.	Crown pos.
Dipterocarpaceae									
Parashorea malaanoan (Blco.) Merr.	N-399	21	0.943	2.89	3.26	1.60	7.74	w	c
Shorea contorta Vid.	N-026	4	0.303	0.62	0.62	0.51	1.75	w	c
Shorea almon Foxw.	N-361	9	2.400	1.44	1.40	4.08	6.92	w	c
Shorea polysperma (Blco.) Merr.	N-025	16	6.362	2.27	2.48	10.81	15.56	w	c
Family total:		50	10.008	7.22	7.75	17.01	31.98		
Elaeocarpaceae									
Elaeocarpus cumingii Turcz.	N-179	11	0.985	2.06	1.71	1.67	5.44	b	c
Elaeocarpus sp. 15	N-619	9	0.280	1.44	1.40	0.48	3.31	b	u
Family total:		20	1.265	3.51	3.10	2.15	8.76		
Euphorbiaceae									
Bischhofia javanica Bl.	N-608	9	0.677	1.65	1.40	1.15	4.20	b	c
Claoxylon brachyandrum Pax & Hofm.	N-615	1	0.034	0.21	0.16	0.06	0.42	?	u
Homalanthus alpinus Elm.	N-193	1	0.009	0.21	0.16	0.02	0.38	b	u
Homalanthus rotundifolius Merr.	N-013	5	0.122	0.62	0.78	0.21	1.60	b	u
Macaranga bicolor Muell.-Arg.	N-695	3	0.070	0.41	0.47	0.12	1.00	b	u
Macaranga tanarius (L.) M.A.	N-184	2	0.102	0.41	0.31	0.17	0.90	b	u
Macaranga sp. 03	N-049	2	0.119	0.41	0.31	0.20	0.92	b	u
Mallotus molissima (Geisel) A. Shaw	N-328	4	0.071	0.41	0.62	0.12	1.15	b	u
Family total:		27	1.204	4.33	4.21	2.05	10.57		
Fagaceae									
Lithocarpus sp. 17	N-550	6	0.490	1.03	0.93	0.83	2.79	m	c
Guttiferae									
Calophyllum blancoi Pl. & Tr.	N-596	2	0.066	0.41	0.31	0.11	0.83	b	c
Garcinia binucao Merr.	N-665	1	0.028	0.21	0.16	0.05	0.41	m	u
Garcinia brevirostris Merr.	N-640	12	1.029	2.06	1.86	1.75	5.67	b	c
Garcinia sp. 22	N-697	1	0.009	0.21	0.16	0.02	0.38	m	u
Family total:		16	1.132	2.89	2.48	1.92	7.29		

Table 1. Continued.

Family Species	Collection Number	No. of trees	Basal area	Rel. freq.	Rel. dens.	Rel. dom.	I.V.	Disp. synd.	Crown pos.
Icainaceae									
Platea excelsa Bl. var. *borneensis* (Heine) Sleum.	N-033	37	4.271	4.74	5.74	7.26	17.74	b	c
Lauraceae									
Actinodaphne sp. 01	N-669	1	0.023	0.21	0.16	0.04	0.40	b	c
Cinnamomum mercadoi Vid.	N-702	2	0.066	0.41	0.31	0.11	0.83	b	c
Litsea luzonica F.-Vill.	N-653	56	7.241	4.33	8.68	12.31	25.32	b	c
Litsea quercoides Elm.	N-470	10	0.380	1.86	1.55	0.65	4.05	b	c
Litsea tomentosa Bl.	N-425	1	0.087	0.21	0.16	0.15	0.51	b	c
Litsea sp. 40	N-687	1	0.231	0.21	0.16	0.39	0.75	?	c
Family total:		70	7.798	7.01	10.85	13.25	31.11		
Legumenosae									
Archidendron clypearia (Jack) Nielsen	N-064	2	0.031	0.41	0.31	0.05	0.78	g	u
Loganiaceae									
Fagraea ceilanica Thunb.	N-693	1	0.039	0.21	0.16	0.07	0.43	?	u
Melastomaceae									
Astronia stapfii Kord.	N-451	3	0.092	0.62	0.47	0.16	1.24	?	u
Memecylon brachybotris Merr.	N-210	14	0.247	2.27	2.17	0.42	4.86	b	c
Memecylon cumingii Naud.	N-452	3	0.572	0.62	0.47	0.97	2.06	?	c
Memecylon lanceolatum Blco.	N-208	17	0.340	2.89	2.64	0.58	6.10	b	u
Memecylon sp. 09	N-699	12	0.455	2.06	1.86	0.77	4.70	b	u
Family total:		49	1.706	8.45	7.60	2.90	18.95		
Meliaceae									
Aglaia rimosa (Bl.) Merr.	N-228	1	0.032	0.21	0.16	0.06	0.42	b	c
sp. 04	N-575	4	0.312	0.62	0.62	0.53	1.77	b	c
Family total:		5	0.345	0.82	0.78	0.59	2.19		
Moraceae									
Ficus benjamina L.	N-632	2	2.523	0.41	0.31	4.29	5.01	b	c
Ficus congesta Roxb.	N-014	15	0.260	2.89	2.33	0.44	5.65	f	u
Ficus chrysolepis Miq	N-069	1	0.423	0.21	0.16	0.72	1.08	f	c
Ficus heteropleura Bl.	N-574	3	0.063	0.62	0.47	0.11	1.19	b	u
Ficus heteropoda Miq.	N-377	1	0.015	0.41	0.16	0.02	0.59	f	u
Ficus irisana Elm.	N-050	1	0.009	0.21	0.16	0.02	0.38	b	u
Ficus minahassae Miq.	N-045	1	0.035	0.21	0.16	0.06	0.42	b	u
Ficus septica Burm. f.	N-474	1	0.011	0.21	0.16	0.02	0.38	f	u
Ficus ulmifolia Lam.	N-032	4	0.051	0.82	0.62	0.09	1.53	b	u
Ficus variegata Bl.	N-379	2	0.052	0.41	0.31	0.09	0.81	f	u
Ficus sp. 18	N-052	2	0.033	0.41	0.31	0.06	0.78	b	c
Ficus sp. 19	N-595	1	0.011	0.21	0.16	0.02	0.38	f	u
Strebus glaber (Merr.) Corner	N-043	8	0.562	1.03	1.24	0.96	3.23	b	u
Family total:		42	4.048	8.05	6.55	6.90	21.43		

Table 1. Continued.

Family Species	Collection Number	No. of trees	Basal area	Rel. freq.	Rel. dens.	Rel. dom.	I.V.	Disp. synd.	Crown pos.
Myristicaceae									
Myristica ceylanica A. DC.	N-639	4	0.237	0.82	0.62	0.40	1.85	b	c
Myrtaceae									
Syzygium garciae (Merr.) Merr. & Perr.	N-447	2	0.196	0.41	0.31	0.33	1.06	b	c
Syzygium gracile (Korth.) Amsh.	N-388	22	1.015	3.71	3.41	1.72	8.85	b	c
Syzygium sp. 27	N-522	15	1.501	2.27	2.33	2.55	7.14	b	c
Syzygium sp. 67	N-698	3	0.275	0.62	0.47	0.47	1.55	b	c
Family total:		42	2.987	7.01	6.51	5.08	18.60		
Podocarpaceae									
Podocarpus imbricatus Foxw.	N-094	1	0.012	0.21	0.16	0.02	0.38	g	c
Polygalaceae									
Xantophyllum discolor Chodat.	N-682	2	0.102	0.41	0.31	0.17	0.90	b	u
Rhamnaceae									
Alphitonia excelsa (Fenzl) Reiss. ex. End	N-156	4	0.205	0.41	0.62	0.35	1.38	b	u
Rosaceae									
Prunus fragrans (Elm.) Kalkm.	N-200	13	1.643	2.47	2.02	2.79	7.28	b	c
Rubiaceae									
Nauclea lanzeolata (Bl.) Merr. var. *gracilis* Ridsd.	N-532	23	1.302	3.51	3.57	2.21	9.28	w	c
Neonauclea calycina (Bartl.) Merr.	N-641	2	0.149	0.41	0.31	0.25	0.98	w	c
Neonauclea sp. 10	N-539	1	0.038	0.21	0.16	0.06	0.43	w	c
sp. 02	N-686	2	0.106	0.41	0.31	0.18	0.90	w	c
sp. 13	N-038	3	0.096	0.62	0.47	0.16	1.25	?	u
Family total:		31	1.692	5.15	4.81	2.88	12.84		
Rutaceae									
Melicope triphylla (Lam.) Merr.	N-382	1	0.008	0.21	0.16	0.01	0.37	?	u
Sapindaceae									
Guioa pleuropteris (Bl.) Radlk.	N-035	2	0.052	0.41	0.31	0.09	0.81	b	u
Pometia pinnata J.R. & G. Forst	N-174	6	0.454	1.03	0.93	0.77	2.73	b	c
Family total:		8	0.505	1.44	1.24	0.86	3.54		
Sapotaceae									
Palaquium sp. 85	N-183	26	4.424	4.33	4.03	7.52	15.88	m	c
Palaquium sp. 33	N-428	19	1.159	3.51	2.95	1.97	8.42	m	c
Pouteria sp. 30	N-152	13	0.507	2.06	2.02	0.86	4.94	m	u
Family total:		58	6.090	9.90	8.99	10.35	29.24		

Table 1. Continued.

Family Species	Collection Number	No. of trees	Basal area	Rel. freq.	Rel. dens.	Rel. dom.	I.V.	Disp. synd.	Crown pos.
Saxifragaceae									
Polyosma verticilliata Merr.	N-523	1	0.006	0.21	0.16	0.01	0.37	b	u
Staphyliaceae									
Turpinia ovalifolia Elm.	N-023	22	2.115	3.51	3.41	3.59	10.51	b	c
Symplocaceae									
Symplocus cochinchinensis (Lour.) Moore ssp. *cochinchinensis* var. *philippinensis* (Brand) Noot.	N-659	1	0.038	0.21	0.16	0.06	0.43	?	c
Symplocus ophirensis Clarke	N-654	16	0.821	2.47	2.48	1.40	6.35	b	u
Family total:		17	0.859	2.68	2.64	1.46	6.78		
Theaceae									
Eurya acuminata D.C.	N-700	3	0.160	0.00	0.47	0.27	0.74	?	u
Ternstroemia megacarpa Merr.	N-215	9	1.060	1.44	1.40	1.80	4.64	b	c
Family total:		12	1.220	1.44	1.86	2.07	5.38		
Tiliaceae									
Microcus stylocarpa (Warb.) Burret	N-044	1	0.022	0.21	0.16	0.04	0.40	b	u
Grewia multiflora Juss.	N-194	1	0.016	0.21	0.16	0.03	0.39	b	u
Family total:		2	0.037	0.41	0.31	0.06	0.79		
Urticaceae									
Dendrocine stimulans (L.f.) Chew	N-173	2	0.032	0.41	0.31	0.05	0.78	b	u
Leucosyke capitellana (Poir.) Wedd.	N-139	1	0.007	0.21	0.16	0.01	0.37	f	U
Family total:		3	0.039	0.62	0.47	0.07	1.15		
Verbenaceae									
Clerodendron brachyanthum Schauer	N-690	1	0.011	0.21	0.16	0.02	0.38	b	u
Grand total:		645	58.8	100	100	100	300		

polysperma with only 16 individuals but 10% relative dominance. An individual of *Shorea polysperma* also had the largest DBH on the plot (180 cm). Other large canopy trees with a DBH of more than 100 cm were *Palaquium* sp., *Canarium asperum*, and *Platea excelsa*.

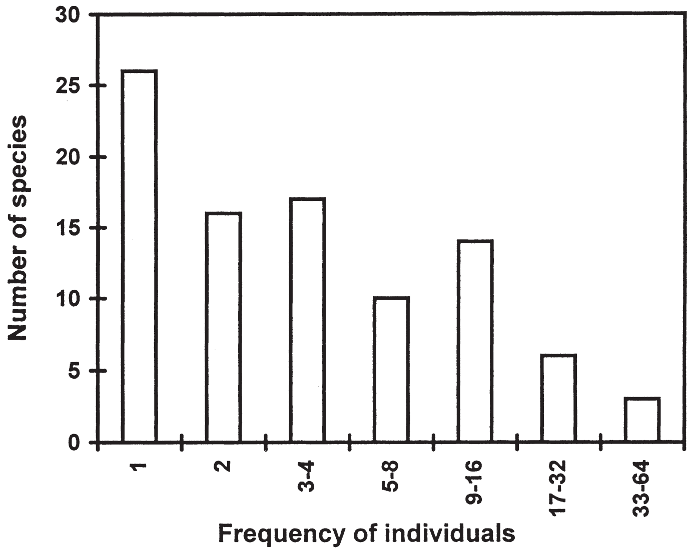

Figure 3. The distribution of the number of tree species in $\log_2$ frequency classes from a 1 ha inventory plot.

Ecological aspects

Fifty-one species were ranked as canopy species, whereas the understory layer consisted of 41 tree species. The understory is mainly composed of species belonging to six families: Euphorbiaceae, Melastomaceae, Moraceae, Myricaceae, Symplocaceae, and Tiliaceae, whereas the important canopy species were members of the families Burseraceae, Lauraceae, Sapotaceae and Dipterocarpaceae.

Trees relying on zoochory for seed dispersal in the canopy and understory accounted for 76% and 96% relative importance, respectively (Figure 4). Wind dispersed species were found only among the canopy species, whereas species with a fruit-bat dispersal syndrome were confined to the understory. Trees with bird dispersal syndromes were predominant in both layers.

Discussion

The widespread use of 1 ha inventory plots and a lower plant size limit of 10 cm DBH allows comparisons of a number of features and statistics with other studies. The basal area in this study is among the highest values reported for a tropical rainforest while the tree density is relatively low which indicates that this forest is in a highly mature stage. Both values are comparable with those of mature dipterocarp lowland forests. A similarly high value for basal area, however, has also been found even at elevations of 2300 m (Pipoly and Madulid 1998), indicating that this measure is not much influenced by altitude. Species richness of this study is in the lower

Table 2. Importance values of the 10 most important species and families. Cumulative percentage of importance values are given in parenthesis.

Species			
Litsea luzonica F.-Vill.	Lauraceae	25.32	(8.4)
Canarium aperum Benth.	Burseraceae	21.85	(15.7)
Platea excelsa Bl.	Icainaceae	17.74	(21.6)
Palaquium sp. 85	Sapotaceae	15.88	(26.9)
Shorea polysperma (Blco.) Merr.	Dipterocarpaceae	15.56	(35.6)
Turpinia ovalifolia Elm.	Staphyliaceae	10.51	(30.4)
Nauclea lanceolata (Bl.) Merr.	Rubiaceae	9.28	(38.7)
Syzygium gracile (Korth.) Amsh.	Myrtaceae	8.85	(41.7)
Palaquium sp. 33	Sapotaceae	8.42	(44.5)
Parashorea melaanoan (Bl.) Merr.	Dipterocarpaceae	7.74	(47.1)
Families			
Dipterocarpaceae Total		31.98	(10.7)
Lauraceae Total		31.11	(21.0)
Sapotaceae Total		29.24	(30.8)
Burseraceae Total		23.15	(38.5)
Moraceae Total		21.43	(45.6)
Melastomaceae Total		18.95	(52.0)
Myrtaceae Total		18.60	(58.2)
Icainaceae Total		17.74	(64.1)
Rubiaceae Total		12.84	(68.3)
Euphorbiaceae Total		10.57	(71.8)

range of values reported for Southeast Asian forests, where the number of species per hectare is typically between 100 and 150 (Whitmore 1995). This, however, is not surprising, since the species richness generally declines with altitude. In a montane forest at 2300 m elevation only 43 species per hectare were encountered by Pipoly and Madulid (1998).

A comparison of diversity measures with other studies in Southeast Asia is somewhat difficult due to the heterogeneity in criteria and methods used. The three diversity indices are only available for one other study in Malaysia (Newbery et al. 1992) and a number of studies in neotropical forests compiled by Bongers et al. (1988). The relatively high equitability index, which describes evenness of abundance of species regardless of the number of species, suggests that no tree species clearly dominates the plot. Shannon’s entropy in this study was among the highest reported, while the Simpson-index, which gives more weight to more abundant species was relatively low, compared to other studies. This indicates, that the species diversity in this forest is to a large extent due to rare species, which can also be seen in Figure 3. In summary no single species clearly dominates the plot, few species are exceptionally frequent and many species are exceptionally rare.

This forest community belongs to the transition zone between the lowland evergreen rainforest and the lower montane forests. It has floristic elements of both forest formations. The presence of Symplocaceae, Cunnoniaceae, Elaeocarpaceae and Laur-

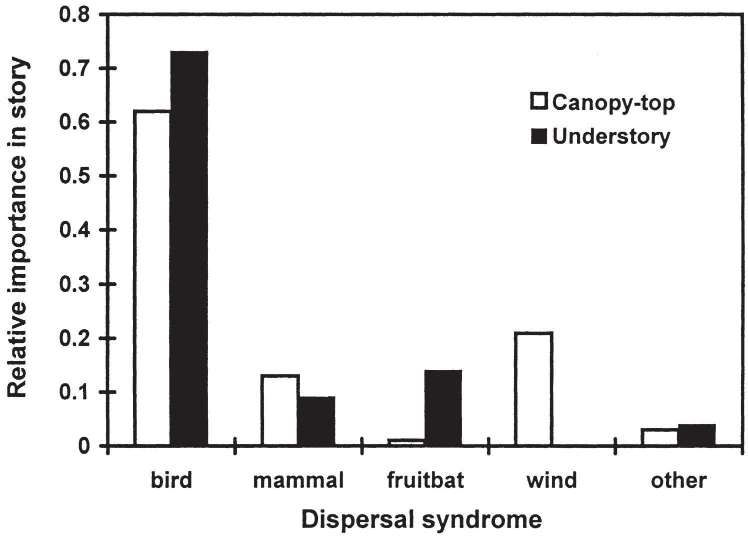

Figure 4. Relative importance of dispersal syndromes for trees of the canopy and trees in the understory.

aceae, and the absence of Leguminosae and Pterocarpaceae are characteristics of the montane forest zone described by Penafiel (1980) and Merlin and Juvik (1994). Nonetheless, this forest is also distinguished from the lower montane forests by its height and the presence of very large buttressed trees. It lacks the high importance of *Lithocarpus* species and conifers described for the lower montane oak–laurel zone by Brown (1919). In addition the presence of Dipterocarpaceae is untypical for lower montane forests, although they are not as frequent as in lowland forests, where they usually account for more than half of the basal area (Whitmore 1984).

Although young trees somewhat obscure the layering of the canopy, two layers can be distinguished in this forest community. The understory comprises fewer species and fewer families than the canopy layer. Whereas it is not uncommon that the understory is dominated by a few species-rich families, this layer normally accounts for most of the species-richness in Southeast Asian lowland forests. The canopy trees usually consist of a relatively small number of species (Kartawinata et al. 1981; Proctor et al. 1983; Newbery et al. 1992). The size limit of 10 cm DBH in this inventory may exclude some understory trees, but our method of distinguishing canopy and understory species is thought to favor a classification of a species as understory tree over a classification as canopy species.

Dispersal syndromes are only useful for a broad assessment of an ecosystem as wildlife habitat, since they are predictive only within certain limits (Howe 1986). Some fruits with bird dispersal syndromes, for example, are also utilized by fruit bats and other mammals. Nonetheless, the great importance of zoochory suggests that for the maintenance of this forest community it is crucial not only to prevent further cutting of trees but also to preserve the remaining frugivore populations. In a detailed study with a limited number of tree species we found that particularly late-successional tree species of the genera *Aglaia*, *Myristica,* and *Dillenia* depend on highly endangered frugivores for seed dispersal (Hamann and Curio 1999).

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